XIV. *Experiments on some Carnivorous Insects, especially the Driver Ant* Dorylus; *and with butterflies' eggs as prey.*

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I have experimented at one time or another during the past few years in the food-preferences of various carnivorous insects. I include in the present paper only my experiments on driver-ants, and those in which insects' eggs were used as prey.

The driver-ants employed were *Dorylus* (*Anomma*) *nigricans*, Illig., var. *molestus*, Gerst., abundant on and about Mount Chirinda in S.E. Rhodesia. In the wet season (November to April) the collector comes across columns of them, particularly in dense forest, where the first intimation of their presence very frequently consists in sudden sharp bites all over his legs—or hers; for on two or three occasions some lady whom I have been escorting through Chirinda has disappeared suddenly into the undergrowth, and I have myself had to seek out some suitable spot further on in which to await her. I say "suitable" advisedly, for once, while striving to free myself of the intruders, I found them literally swarming all over me, and realised too late that in my haste I had sat down to search for them in another part of the same highly populous column.

The main column sometimes marches as many as twelve or fourteen abreast: I do not of course mean to imply that the ants are in definite lines. It is margined on each side, however, by a line, serried or broken, of grenadier-sized guards, each facing outwards with great uplifted mandibles or patrolling about on the flanks. Within the column there is usually a current in both directions, but very commonly mainly in one; and smaller "loop" columns help to prevent congestion and to serve, apparently, other special purposes. Over a foot, or, it may be, much more, of the ground on each side wander scattered stragglers that seize on any potential prey, from a minute beetle to a cow, that is so foolhardy as to approach them, and, aided, when struggling attracts attention, by the

other ants near, drag it (if they can) into one of the columns. It is these stragglers that, in my particular experience, are the more frequent mark of the fly, the habits of which have been described by Mr. W. A. Lamborn (Proc. Ent. Soc., 1913, cxxiii–cxxviii).

Following the column, as it winds through the forest or over the grass-country, we may at last come to a place where the ants are scattered in hundreds of thousands everywhere, and are definitely searching—all over the ground, up the grass-stems, and up, sometimes for some distance, even the stems of trees. It is under these circumstances that I have on a few occasions, with insects abundant, been so fortunate as to witness the scene that Thomas Belt described so graphically, in connection with *Eciton predator*, in his fascinating "Naturalist in Nicaragua"—the seizure of the fleeing insects, the eventual overpowering of even grasshoppers, the clustering of the prey on the tops of the herbs and grasses, and its drop into the thick of the ants below when approached by those that climbed after it, and the escape by suspension of spiders and larvae. I have also on a few occasions watched birds attending *Dorylus*, as Belt says they attend *Eciton*, to rob stragglers of their prey, and for the sake of the flying and hopping insects flushed by the ants. Some of the birds on occasion eat the ants themselves. In my experiments on many species of insectivorous birds I found that some ate ants generally, including *Dorylus*, far more readily than others. Of these others some showed a strong repugnance to them, and it is doubtless in relation to this latter class of enemy that ant-mimicry finds its main use. Yet even the birds that prey on ants show caution in attacking *Dorylus* in column, merely (in my observations) dropping down to stragglers and hastily returning to their perch.

Ants of other species become very uneasy when drivers are near, and the carrying out of the contents of their nurseries by those that inhabit my verandah posts has often been a warning of the necessity for putting on pots upon pots of water to boil. Not that it is with anything but reluctance that one pours boiling water on these animals, so useful when they confine themselves to the Kaffirs' quarters, the kitchen, and the kitchen garden. But it is unpleasant to have to turn out at a moment's notice, at night, oneself; and, in my case, numerous live birds in cages in the verandah had to be protected from

an enemy that would have made short work of them. *How* short, is suggested by the following incident. Some years ago (1902–3) three goats died under circumstances that suggested meat hunger on the part of my Kaffirs. Not to gratify them, I pretended to poison the carcases (using only salt, however), and placed them out in a lonely part of the Chirinda forest "to kill wild beasts." I might have spared even the salt, for they speedily became protected against the most venturesome native—or "wild beast"—by a dense, black, seething mass of "Idunga." They remained so for only a very few days. Then the ants resumed their more normal avocations, and left three skeletons behind them. It sometimes happens too that great stampeding is heard in the kraal or shed at night amongst whatever animals are enclosed in it, and, going out gun in hand, expecting perhaps to find that leopards have broken in or that lions are trying to make the animals break out, one finds the place full of—drivers.

I have on one or two occasions found quantities of chitinous *débris*—of millipedes, grasshoppers, beetles and other animals—mixed with earth in a heap outside what seems to be, at any rate, as near an approach to a permanent habitation as these ants employ; and once, in my garden, my foot suddenly went through and revealed a hole, perhaps eighteen inches deep, which was full of the driver-ants, though, it being in the dry season, it was long since I had seen them about. I could hardly have investigated properly without cyaniding them, and I did not wish to lose the protectors of my garden; but the discovery, and the fact that on several subsequent occasions I found them still there, suggested that they do possess headquarters and occupy them for prolonged periods.

It struck me early in 1911, when *Dorylus* was specially active in the neighbourhood of my house, that it would be interesting to ascertain whether any non-flying insects are protected from these marauders. I accordingly carried out the experiments I shall describe first. Two years later I carried out the experiments with butterflies' eggs.

I had found, in the numerous experiments on many insect-enemies in which I had used adult insects as prey, that not only do differences in acceptability exist, some species being obstinately refused while other species are eagerly eaten, but that the finest gradation exists between those insects (Z) that are only accepted when the enemy

is hungry, though Y, X, W, etc., refused in turn as he fills up, to the few species (A) that are regularly eaten by him at all stages right up to repletion-point.

This fine grading in degrees of palatability was unexpected—though Mr. Marshall's experiments had shown that *some* grades might be looked for—and, starting with a bias in favour of the "palatability" of most *Nymphalinae* and *Pierinae*, I at first fought against it; but I could not long withstand the combined testimony of every animal I experimented on.

Fine gradation in palatability granted, with its corollary that few species are at all times acceptable to all their enemies, it was interesting to note its theoretical bearing. This seemed to be, that there are probably few species that do not sometimes require to be distinguished by an enemy from such other species (or, an important and highly explanatory consideration, from their own parent form) as are at the moment acceptable to him. The selective factors would be the unmistaken refusals and the mistaken attacks of enemies, adult and otherwise (for I find that even the former go on all their lives making numerous mistakes and that they also tend to test specially anything of unusual appearance).

Yet distinctiveness and diversity are nearly as marked in the eggs of Lepidoptera as they are in the fully developed insects that lay them.* These eggs are laid on exposed surfaces liable (as I have many hundreds of times seen) to the *exceedingly* close scrutiny of small warblers, white-eyes and other minutely-searching enemies; they are often in contrast to those surfaces and are commonly, even when not thus in contrast, distinctive; and this distinctiveness is apparently in part for visual effect, for it is absent from the hidden bases of the eggs, nor is it approached by that of most underground eggs known to me, the differences between which are merely such as might naturally result from the fact that their parents are different. I thought, therefore, that it would be interesting to ascertain whether nauseousness—and graded nauseousness at that—was present in leaf-laid eggs.

I was very unlucky in my attempts to secure a suitable

* I lay stress on *distinctiveness*—recognisability when detected—rather than on *conspicuousness*, for I regard the latter as a purely auxiliary quality, though highly useful and likely always to be selected so far as it can be safely carried.

animal on which to experiment. Two or three broods of small warblers that I tried to rear failed, and I could not secure a fully-grown bird of a suitable species. Finally I had to use driver-ants, unsuitable in so far as they possess no sight, yet suitable in their general apparent readiness to eat any animal substance, and in the fact that they must very commonly indeed meet with lepidopterous eggs when searching the herbs and lower shrubs on their foraging expeditions. I also tried other insects—cockroaches (suitable mainly in the fact that they are credited with the readiness to eat or, at any rate, try any food of an animal nature), a carnivorous ladybird (*Alesia bidentata*) and a cricket (*Arytropteris* sp.), which has often been a great nuisance to me, devouring insects of many kinds that I have left on the verandah table.

Obviously the animals were not perfect for my purpose; yet I felt that *rejections* by the drivers, the cockroaches and the cricket, also any preferences any of them might show, would at least, for the reasons I have indicated, be suggestive, though of course by no means conclusive. I therefore carried out on them the experiments which I shall describe.

A few remarks on the eggs used are comprised in the concluding section of this paper.

Note.—I have mentioned the fine grading of prey that occurred in my experiments on insectivorous birds, wild and tame, and the suiting of the capture or acceptance to the exact state of appetite of the moment. I show a diagram to illustrate these "layers" of appetite. It is also true (and this too has an explanation bearing on Dr. G. D. H. Carpenter's highly-interesting observations, read to-night *) that a rapidly digesting animal may go on eating a fairly low-grade insect (such as I have found many Lycaenids to be), or even *very* low-grade species, indefinitely, with occasional short intervals, if higher-grade prey is not available in sufficient quantity to carry it to a more advanced stage in the process of filling up. Thus a swallow of mine ate more than 80 *Neptis* and a small hornbill (*Lophoceros*) more than 50 *Danaida chrysippus*, in each case in quite a short space of time; a rest of a few minutes after each refusal, accompanied doubtless by subsidence, rendering the bird's digestive apparatus capable of dealing with three or four more. The swallow

* Proc. Ent. Soc., 1915, p. lxiv.

even ate more and at least as great a weight of *Neptis*, when thus verging continuously on the *Neptis*-refusing point, than it did of the better-liked *Pyrameis* at far nearer repletion-point in the same space of time. The possible bearing of this on some of the observations in which a bird has been seen preying continuously on *Danainae* is obvious; and a long-ago expressed view of Prof. Poulton's, based on his own experimental results, is also borne out—that it is only in the presence of pleasanter insects that unpleasant species will derive advantage from their special defence.* My experiments have shown, however, that it is a matter of relative indigestibility rather than of unpalatability, that a bird can digest species of prey when hungry that fail to stimulate the digestive secretions when it is fuller, and that a bird, enabled like my swallow and *Lophoceros* by a rapidly working digestion to prey fairly continuously on low-grade prey, probably never approaches repletion-point while doing so.

1. Experiments on *Dorylus* (*Anomma*) *nigricans*, var. *molestus*

April 26th, 1911.—A large stream of driver-ants was flowing in both directions between two tunnels, at the foot of a steep bank and under the verandah curb respectively.

I put down in the middle of the stream four *Mylabris amplectens*, Gerst., two *Amauris albimaculata*, killed by myself as I put them down and smelling strongly of ordinary gas, three *Epilachna polymorpha*, Gerst., and a *Zonocerus elegans*. All were at once overwhelmed by the drivers, and for some minutes remained so. Ten minutes later I found that the numbers clustering round the four *Mylabris* and the three *Epilachna* had thinned considerably, but the ants were still in masses on the *Zonocerus* and were busily engaged in cutting off the wings of the *Amauris*. A *Belenois* that I now put down was attacked at once, its wings cut off and left lying, and its head, thorax and abdomen carried into the bank "drive" before either *Amauris* was ready to follow it. A *Rhopalocampta libeon* was at once seized and carried along bodily, its wings being removed while it was in motion, and the two *Amauris*, their wings left where their owners had first been put

* Proc. Zool. Soc. Lond., 1887, p. 191.

down, followed it, also in sections. By this time the ants had entirely abandoned the four *Mylabris* and the three *Epilachna*. One of the former was on its back motionless, another was remaining quite still—head held down—in the centre of the stream of ants; many of them felt it with their antennae as they passed, but no attack was made on it, and the other two as well as the three Epilachnas were calmly marching off. They drew attacks in doing so from the ants they passed, and the two *Mylabris* in particular were occasionally overwhelmed for a moment and perhaps dragged back a little. But they were always abandoned again after a time and they made good their escape. I took them up and found that both *Mylabris* were still able to expel juice fairly freely, the *Coccinellidae* (with one exception, not, however, so freshly caught when given), apparently not. The *Zonocerus* continued to be the centre of attraction for large numbers of ants, but they were making very little headway in the process of its dismemberment.

I now inserted four larvae, one of *Papilio demodocus* at about the end of the brown-and-white stage, one of *Amauris albimaculata* (about $\frac{1}{3}$ grown) and two of *Acraea acara* ($\frac{1}{4}$ and $\frac{1}{3}$ grown respectively). All were at once surrounded, but the attack on the *Amauris* larva was not of a very formidable nature: the ants used their antennae rather than their jaws and evidently disliked it intensely, for they very speedily abandoned it entirely. In making off, which it did apparently quite undamaged, it drew a few attacks, but these proved to be no more formidable than the first, and the larva was each time quickly abandoned. The *A. acara* larvae were more seriously attacked, but the ants had the greatest difficulty in getting "in" at them, the much-branching spines beaded at all the extremities with the yellow protective juice everywhere barring their way. A number of these spines were in each case shorn by the ants (some close off to the skin) during the attack, but they finally abandoned both larvae, and, though I frequently replaced both these larvae and that of the *Amauris* in the centre of the ant-column during the remainder of the experiment, the subsequent attacks, when any were made at all, were less serious than the first, and the larvae were each time allowed to escape. Very different was it with that of the *Papilio*. It at once extended its red filaments on being attacked,

but though the one or two ants in their immediate neighbourhood retreated for the fraction of a second they at once closed in again, and, overwhelming the larva, carried it speedily along (a distance of about three feet) into the verandah drive. A hive-bee at this moment came tumbling into the "drivers" from above. It was at once seized by the leg by one of the larger warriors, and remained tumbling over and over and drawing more enemies. I noticed that it extended its sting, but only to have it seized and tightly held by one of the drivers. It was quickly subdued, and when I last saw it was being carried in the direction of one of the drives. I now placed a large *Danaida chrysippus* in the column, first killing it. The ants at once persistently attacked it, and, having carried it just outside the column, commenced to dismember it. A smooth moth larva with a velvety appearance and conspicuous black and white bands (*Aletis*?), not uncommon in the forest, was seized, and after a very great deal of delay carried along to the bank drive, though the ants again refused the *Amauris* and *Acraea* larvae. It had been three days in captivity without my having been able to find its food-plant and was undoubtedly weakened—probably in its protective qualities too. A *Papilio echerioides* ♂ was broken up, its wings left lying, and its more material parts carried in sections to a drive. A small Sciarid fly with black wings and a red thorax (*Apelmocreagis thoracica*, Macq.) had been settled on the ground right amongst the ants, neither taking any notice of them nor drawing an attack. I captured and disabled it and placed it back amongst them, but though numbers, I might say hundreds, inspected it, often passing their antennae over it, all moved on and no attack whatsoever was made. But an Arctiid moth, *Rhodogastria bubo*, was at once attacked and its wings stripped off where it lay. It had unfortunately exhausted its foamy thoracic exudation previously to being placed amongst the ants: this might have made a difference. A *Mycalesis campina* was at once carried along, as were also a second *Danaida chrysippus* and a *Byblia ilithyia*, their wings being stripped off *en route*. It was now an hour and a quarter since the experiment commenced: the *Mylabris* left in the column was still in the same place uneaten but motionless, and no longer noticed by the ants. On my taking him out he immediately commenced to move about, but dragged three legs

after him : the two previous *Mylabris* had escaped to all appearance quite without damage excepting for a slight wound on an abdomen. The fourth *Mylabris* had, as I ascertained, quite exhausted its juice. It had latterly been receiving a good deal of attention from the ants, which were at this moment busily cutting off one of the elytra and were carrying its owner along. They soon abandoned it again, but when I removed it later I found it to be dead. The large ♀ *Zonocerus* was lying where originally placed, but had been reduced a good deal and was still a great centre of attraction. The small fly was still lying neglected in the midst of the ants. A *Mylothris rueppelli* was now broken up and carried off, as were, without breaking, a housefly and a common cockroach. Three of the ants themselves which I killed and put back in the column were felt by large numbers of their comrades, but always passed by until suddenly one smallish ant, coming across one of them, seemed to think it her duty to lift and carry it along. I removed one of the other two and placed it in another ant-army of the same species which was busily crossing a garden path at a considerable distance away, with, as so often, a drive at each side. It, too, was neglected for the three or four minutes during which I watched.

The first ants had shown no special ferocity towards myself, but this second party at once attacked me, and I had to keep a sharp eye on my feet. Judging that they might also be in the mood to take more highly unpleasant insects than their comrades had accepted, I brought over an *Epilachna*, a *Mylabris* (adding a second from the two that had escaped), the small fly, the *Amauris* larva and one of the *Acraea* larvae ; all these were still being neglected by my first band of ants. Placed just beside the column all were at once attacked furiously. The *Acraea* larva (it was the larger one) was gradually shorn of spines and finally carried into a drive, as were *both Mylabris* and the Coccinellid. The *Amauris* larva was attacked just as furiously and was apparently freely bitten, for blots of greenish black juice sprinkled the ground on either side of it. These seemed to fall just *away* from it : were they *emitted*, *e. g.* by the filaments ? But the original attackers gradually desisted and left it, though it was still for some time attacked by groups of ants that apparently came across it for the first time. Finally it was left alone

entirely, and, looking back at it at the end of the *Acraea* larva incident I was surprised to find it half-covered with little heaps of tiny fallen leaflets from an overhanging *Acacia baileyana*. Watching, I saw several leaflets and in one case a portion of a midrib with a few leaflets attached brought up and placed on it by the ants. The fly had appeared to be attacked for a few moments with the same vigour as were its fellow victims, but evidently the onslaught was not with pointed weapons, for apart from the loss of a wing it seemed to have sustained little or no damage when the ants abandoned it. It lay in the midst of them and, whenever I moved it, was at once set on to by the ants, but they quite evidently had no use for it and each time speedily desisted. The fact that the two *Mylabris* had already undergone an ordeal at the hands of Column No. 1 and that one of them was certainly destitute of "juice" might, I thought, account sufficiently for the comparative readiness with which they and, for that matter, the *Epilachna*, had been taken. I thereupon captured (within a few yards of the column) two more, also just afterwards a fresh *Epilachna*, and at once, as I did so, put them in. I happened to drop one *Mylabris* close to a vertical shaft that was guarded at its mouth by a large number of ants. It was at once pulled in. The second, placed further along, was attacked with great fury and carried along for some distance, then partially abandoned, then attacked again and so on. Finally, after a considerable time, it was left out to one side of the column and partly covered over with leaflets like the *Amauris* larva. The latter had now emerged from its covering and was crawling towards the column. It was attacked three or four times, particularly when it arrived at the column, but never very seriously—the ants mostly desisted directly they came into contact with it—and it passed out on the other side. On picking it up I found that it seemed not greatly the worse for its experience. The front pair of filaments were hanging down limply and all the others were partially collapsed, but on my setting it on a leaf of its local Asclepiad food-plant (*Cynanchum chirindense*, S. Moore) it at once commenced to eat. The fly, put down again, was treated with the same respect as previously. But a large beetle, *Psammodes* sp., now introduced was attacked furiously and was quickly concealed under a mass of ants. Nevertheless, it gradually crawled

away, the ants lessening as it went, and on getting off the open path and passing through some vegetation it succeeded in brushing off most of those that remained. It was greatly incommoded by them, and kept stopping to brush them away with its forelegs from its palpi and antennae. When I finally recovered it, several yards from the ant-column, only three ants were left clinging to it, and it seemed to have been effectively saved by its armour from all injury. The *Epilachna*, I should have mentioned, was attacked vigorously for a time, and afterwards for a longer period in a desultory fashion. It at first remained adpressed closely to the ground, and the ants plied their mandibles in vain over the glossy surface of the elytra; then one or two pushed under and turned it over, and it was carried along a few inches. This sort of thing went on for some time—I could not see that it made use of any juice it may have possessed. In any case, the ants made very little impression on it, and did not shift it very far from its original station.

At this point, having just captured a passing *Acraea neobule* ♂ and an *A. natalica*, dull ♀, I went with them to Column No. 1, and found the last remains of the *Zonocerus* disappearing into the drive. I removed a forewing of *A. neobule* and placed the butterfly amongst the ants. Disabled even to that extent it seemed to have no difficulty in its flutterings in shaking off such as clutched it, and a butterfly of its size, able to fly, would, I have little doubt, experience very little trouble in getting away from a crowd of drivers amongst which it had inadvertently landed. I killed it and replaced it. There was quite the normal amount of juice, but the ants made as short work of it as they had done of *Amauris* and *Danaida*, separating the wings from the body and carrying the latter into their tunnel. They then refused, in the same manner as before, to eat the *Amauris* larva and the fly, attacked a *Mylabris* and desisted, then attacked and carried in the *Acraea natalica*. It too possessed a normal amount of juice, and small drops of this exuded at the nervures when I cut the wings off.

Returning to Column 2 I found the *Mylabris* and the *Epilachna* in the same place. I put down two coffee-bugs (*Antestia variegata*), a small weevil (*Systates* sp.) common in coffee, and a beetle, *Himatismus fasciculosus*, Pér. The weevil was carried to a drive at once. The bugs caused

delay and were carried hither and thither a little, but finally brought to the main track and taken to a drive. When I last noticed *Himatismus* it too was being dragged along. I then put in eight *Antestia variegata* and eight weevils. All were seized—it was impossible to see whether one was preferred to the other—and carried along.

I now went back to Column 1. It had moved on to some extent, and a number of its members were busy exploring, and apparently enlarging, a vertical hole in the ground, out of which I saw them bring up three white bee larvae. A number of large guards were stationed in a mass over the hole, and a thin stream of ants passed between these and the bank. On the other side the stream was thinner still. I put an *Antestia* on each side. That away from the bank was once or twice attacked half-heartedly and was inspected by a number of passing ants, but on the whole left alone. Very different was the treatment accorded one of the bee grubs. I placed it beside the bug, and it was at once seized and carried off, several ants joining in. The bug continued to be ignored. The other bug, however, had been seized and carried to the mass of guards. One of these seized it, and straddling over it carried it back the way it had come, and finally disappeared with it into the hole in the bank.

Returning to Column 2 I found the *Epilachna* and *Mylabris* still in the same place, and I was just in time to see the last bug and the last weevil disappear into the drive. I should have said that before I left, the *Epilachna* had more than once escaped, practically unmolested, from the ants, but that I had each time put it back. I now put in five fresh *Mylabris amplectens* and a smallish *M. oculata*. Considerable excitement ensued amongst the ants, and the beetles were being dragged hither and thither, when a large reinforcement, including a considerable proportion of the largest workers, emerged from one of the drives, and, seizing the beetles, including the *Epilachna*, carried all along, often with a great deal of delay, into the opposite drive. One beetle only withstood the attack, and that was the original *Mylabris amplectens*, a very large specimen. It was attacked like the others, but relinquished, attacked again and again, left, and so on, until at the end it was not much nearer the opposite drive than it had been before. The *Amauris* larva, the remaining *Acraea* larva and the fly, which I put in once more, were treated

much as on previous occasions, and finally left high and dry. But the rush was already lessening somewhat by the time they were inserted, and a little later, when the column had subsided to its normal dimensions or rather less, it took very little notice of three more coffee-bugs and soon abandoned them completely, though a small Elaterid was at once seized and hurried along to the opposite drive.

Meantime, the other party had established better "through" communications once more, and though comparatively few in numbers seized and carried off into the bank eight coffee-bugs, three weevils and a *Harpactor erythrocnemis* (also taken in coffee), though still ignoring to the same extent as previously the *Amauris* larva and the fly. They attacked a small *Mylabris amplectens*, but eventually abandoned it.

Later, having captured a fine ♂ *A. areca*, I returned the *Amauris* larva and the fly to Column 2, where a large number of ants were passing. Both were treated as before. Two Epilachnas were attacked, but eventually abandoned and gradually allowed to escape; the original *Mylabris amplectens* was still present, drawing an occasional slight attack, but was mostly left alone; a dead *Dorylus* was ignored for a while, but then picked up by one ant and carried along; the *Acraea* larva was attacked, but allowed to escape. Afterwards, as it was moving along parallel with the column, I was amused to watch it meet a large number of ants. As each stopped and felt it with its antennae the larva would stop dead. When the ant moved on, as it invariably did at once, the larva would move on too. There was no further attempt at an attack. A small piece of banana pulp that I put down was attacked, several ants making off to the drive with portions of it, and an ordinary cattle tick (*Rhipicephalus* sp.) was seized and carried to a drive, but not until it had inconvenienced its carriers very greatly (three in all carried it, but only one at a time) by getting under them and clinging to their legs. A coffee-bug was seized and carried along. Then *A. areca*, with wings shorn $\frac{1}{3}$ of the way up and exuding juice, was placed amongst them. Even in this condition it was too active for them, so I killed and returned it, when it speedily became a seething mass of ants. I put down just afterwards an *Amauris albimaculata* with its wings attached and a coffee-bug. The latter appeared

to be attacked somewhat less readily than the two butterflies, but once definitely seized was carried along fairly fast; the *Amauris* was dragged wings and all, and, considering that it made a broad and heavy load, proceeded with considerable speed. It was at the hole and in process of being diswinged there before the *A. areca* had travelled more than three or four inches. I had noticed at first three or four ants withdraw on coming into contact with the liquid exuding from the nervures of the Acraea's wing-stumps, but the butterfly's juices, though normal in quantity, were either insufficient or not unpleasant enough to keep its enemies off. At this moment a fresh rush occurred, and I at once returned the two Epilachnas, the *Mylabris*, the two larvae and the fly to the main track. The two ladybirds were at once carried off into the drive, as was, after more in the way of hesitation and temporary abandonments, the *Acraea* larva; the *Mylabris* was carried to the mouth of the drive, but as I saw him crawling about that neighbourhood half an hour later was probably abandoned there or just inside. Considerable disinclination was still shown to attack the *Amauris* larva, and it was only by moving it frequently in their midst that I irritated them (for that I presume was it) sufficiently to make them really attack it. When they did, they attacked with the utmost ferocity, and having killed or practically killed the larva, carried it along to the drive. I rescued it at the last moment, wishing to use it further. It had this time emitted no dark juice.

Similar, if not greater, disinclination was shown to attack the fly, but finally this, too, was seized and carried along by one big warrior. It was still a considerable time before the *A. areca* reached its destination, and was there broken up and carried in, but there was never any abandonment of it; it was always covered with ants.

At about this stage I again put in the *Amauris* larva, and, on the magnifying glass to which it was attached a freshly pupated individual of *Amauris albimaculata*, somewhat crushed accidentally. The ants refused the larva, and though numbers swarmed upon the glass to the pupa all retreated on coming into contact with either it or its fluid, and no attempt was made to carry if off. I tasted the fluid; it was to me reminiscent simply of raw leaves of no very definite kind.

Later, having again ascertained that the ants would not

touch the *Amauris* larva, though an imago of the same species was at once carried along, I interrupted the column by placing in its midst a rather spread-out mass of not less than 200 coffee-bugs thoroughly mixed up with about a third of that number of the weevil *Systates* and a few *Himatismus*. Half an hour later the pile had been reduced by about half, the ants taking the insects as they came from the outside and not choosing between weevils and bugs. An hour or more later, by lantern light, I found the column reduced to almost nil and the bugs to between twenty and thirty. They were somewhat scattered and more or less piled up between with loose earth and *Acacia* leaflets, a very scanty layer, however. No weevils or *Himatismus* were left. I inserted an *A. albimaculata* and a *Leuceronia thalassina* ♂, but the few smallish ants that were still using the track took no notice of them, beyond stopping to inspect *en passant*. Shortly afterwards I noticed that a fresh track had been made alongside the old one, and more ants were passing along it. The old one with the butterflies still in it was now quite deserted. I placed them together in the centre of the new track, about equidistant from each drive, and saw both seized. On returning a few minutes later I found them being dragged in opposite directions. The *Leuceronia* was going at unmistakably the better pace and had already practically reached its goal; the *Amauris* with about the same number of ants was barely half-way. Now, ten minutes later, as I am about to go to bed, the *Amauris* has only proceeded about two inches further. I had removed the *Leuceronia* on my last visit, wishing to use it further; it was then within an inch of its hole. The ants had made no attempt to strip the wings off either.

April 27th, 1911.—I looked once more, for the last time, ten minutes after the above was written. The *Amauris* had only proceeded another two inches in spite of the fact that since I removed the *Leuceronia* the number of ants engaged on it had more than doubled. They seemed to be spending as much of their time in feeling over the surface of the butterfly as in carrying it. The bugs, though a number of ants was passing round them, were being completely neglected.

This morning the wings of the *Amauris* were lying just outside the drive.

Later: Found this afternoon where the above drive

emerged, ten yards away, four or five of the bugs lying abandoned though continually passed by the ants. At the spot experimented at yesterday the 20–30 bugs are still lying untouched, though a large stream of ants is passing them. I put in a *Rhodogastria bubo*, just captured and commencing to exude froth. It was at once seized by the legs and commenced to froth most lavishly; but though the froth certainly discommoded such ants as came into contact with it, it was confined to the thoracic region, and the rest of the moth was quickly covered with its enemies. Also, in its struggles, the mass of froth was quickly knocked off and no more was forthcoming. I rescued it at this point and had to pick a large number of drivers from its legs.

On the coffee-girls bringing in their daily kill of bugs (*Antestia variegata*) again this evening, I placed a few in the ant-column close to where the remains of yesterday's still remained untouched; also an *Epilachna hirta*, just captured. The latter only was attacked, but never seriously, and was twice allowed to escape. I noted that such ants as came into contact with the protective fluid drew back slightly, but I also noted once more their failure to grasp or pierce its glossy elytra with their jaws. It would be interesting to see whether the fluid without the glossy hardness of the beetle's exterior would be a sufficient protection.

On, I think, the following day—April 28th—I found large numbers of *Antestia* thrown out of the drive, at the mouth of which four or five were lying on the 27th. None of the beetles taken with them had been thrown out.

May 12th, 1911.—A column of *Dorylus* was busily exploring the recesses of an old post to-day, and dragging out thence the larvae of wood-boring Hymenoptera. I placed in their midst eighteen full-fed cattle-ticks (*Rhipicephalus*, sp.). They were at once smothered in masses of the ants, but fifteen minutes later, though still lying in the midst of the column, they had been abandoned completely. They were apparently undamaged. One of my ground-hornbills (*Bucorax caffer*) stalking along shortly afterwards ate them all, but took no notice of the drivers.

Yesterday when I was cutting up a sheep, and throwing an occasional waste bit to the hornbills (*Bucorax caffer*), I threw one such piece into the midst of a column of

"drivers." It was at once covered with the ants, but a hornbill at once strode up, picked it out and, after shaking off only a few of the ants, swallowed it with all the rest that were clinging to it.

Remarks.—The ants were unconfined, carrying on their ordinary daily avocation. The experiments cannot therefore be criticised as having been carried out on animals under "highly unnatural" conditions. Yet the ants showed strong "preferences," readily taking some animals when they would not take others at all, and when failing in their attacks on yet others. It is true that some of the winged insects offered were, because winged, not such as the ants would normally have an opportunity of seizing except when hunting at night—but they do hunt at night greatly. Most of these were nevertheless taken by them, and, even if we should exclude these as not forming a part of the ants' normal food, we should find that a number of species were offered that the ants must meet with continually, and that very strong "preferences" were shown even as between these.

The butterflies tested, the moth *Rhodogastria bubo*, the larva of *Papilio demodocus*, a hive-bee, the larvae of a bee and of a wood-boring Hymenopteron, a cockroach, the beetles *Himatismus*, *Systates*, and an Elaterid, and a *Zonocerus elegans* were probably all less protected from *Dorylus* than even the weakened larva of *Aletis monteiroae*, and certainly than the larvae of *Acraea acara*, than adult *Mylabris amplectens*, *Epilachna polymorpha* and *E. hirta*, and *Antestia variegata*, and all these, apparently, than the fly, the larva and pupa of *Amauris albimaculata* and the beetle *Psammodes* (protected by hardness). But the ejection from the tunnel of a large number of *Epilachna* a day or two after they had been taken in may indicate that these were found to be as bad as any of the objectionable species. Certainly the ants found the fly and the Danaine larva and pupa much more *obviously* unpleasant than the Epilachnas, *Mylabris*, *Antestia*, and *Acraea* larvae, and it is clear from an experiment to be described below that the latter when well-grown are acceptable enough to them if they give the ants time, and the latter are persistent enough, to raze the juice-dealing hairs.

The butterflies used were *Danaida chrysippus*, L., *Amauris albimaculata*, Butl., *Mycalesis campina*, Auriv., *Acraea neobule*, Dbl. and Hew., *A. egina*, Cram. var. *areca*,

Mab., *Acraea natalica*, Boisd., *Byblia ilithyia*, Drury, *Mylothris rueppelli*, Koch, a *Belenois*, *Leuceronia thalassina*, Boisd., *Papilio echerioides*, Trim., and *Rhopalocampta libeon*, Druce. It seemed that the Acraeas gave a little more trouble, with their juice, than did *Amauris* with its pungent smell, yet this did not save them even for a moment. That *Amauris* in time may have been better protected than *Leuceronia* (and probably others) seemed to be suggested by the slowness with which the ants would progress with it, "spending as much of their time in feeling over the surface of the butterfly as in carrying it." The froth-masses of *Rhodogastria bubo* and the bay-leaf-scented filaments of the larva of *P. demodocus* were only momentarily and locally deterrent, and the sting of the hive-bee not at all. The *Zonocerus* with its (to us) nauseous smell and its ill-effects on vertebrates eating it, was naturally more slowly dismembered than the smaller species used, but that was all. Quite unprotected also, apparently, were beetles *Himatismus*, *Systates*, and the Elaterid, the cockroach, the hymenopterous larvae, and adult *Musca domestica*. A hungry cattle-tick was taken, though full ones, on another occasion, were all refused; but a very interesting incident in the experiments that follow should be seen in this connection.

The acceptance of vegetable-matter (banana) was interesting, as was the fact that even partly-disabled Acraeas—not the most active of butterflies in any case—were able to escape for a time from the drivers. With power of flight they should never be taken except when asleep. This consideration, with the *special* repugnance shown to eggs and very young larvae in the experiments still to be described, suggests a very beautiful instance of the probably universally obtaining principle of compensation and complementation and of the fact (implied therein) that an animal's defences may vary greatly at different stages of its existence, one defence being donned in proportion as another is doffed, and *vice versâ*. Thus in both *Acraea* and, say, *Papilio dardanus*, numbers and intrinsic nauseousness, at their height in the egg-stage (assuming the experiments to be reliable), and then most necessary, are gradually exchanged, in the first case for an ever-growing supply of protective fluid, in the second for an ever-increasing procryptic element in the coloration, this culminating in the extraordinarily complete resemblance

to a growing Rutaceous leaf displayed by the pupa. Each emerges. The *Acraea*'s fluid-supply has been much decreased, yet is efficient enough in relation to present enemies, and its flight is sufficient to commonly save it from the driver. The *Papilio* has flight, and, instead of a protective fluid, has polymorphic mimicry in the female (compensated in the male by better flight and slightly greater nauseousness), and a strong procryptic element in the "matching" of the dulled underside by both sexes in resting. I have already mentioned the native view of nestlings, and I am publishing elsewhere ("Ibis") the results of some actual experiments with birds' eggs: a stronger procryptic element, represented most usually in the *nests*, is present here than in the case of butterflies' eggs; also parental protection; so that nauseousness is to a varying extent less necessary, though it is often, I believe, in some degree present to complement or replace these other defences. Those plants in which the seedlings are less liked by herbivora than is the adult foliage (protected by height, etc.) afford a somewhat closer parallel. though they trust more than even butterflies to their reproductiveness. It would be very interesting, in view of recent observations that have discredited the view that it is myrmecophilous, to ascertain whether the bull's-horn thorn acacia of America is not one of them.

Further interesting points in the experiments were: (1) the effect on survival of, *apparently*, variability in juice production or conservation in individuals of *Mylabris*, one such individual, a large one but amongst the first to be inserted, remaining protected to the end, while others were taken and one was definitely exhausted of juice and killed; (2) the shearing of the spines of *Acraea acara* larvae. This was improved on in a subsequent experiment in which the juice was absorbed by the application of earth-crumbs. I have on a few occasions seen *Acraea* larvae feeding with similar earth-crumbs attached to their bristles, and there can be no doubt that the ants' successes against Acraeine larvae in these experiments were mainly due to my replacing the escaped larvae amongst them time after time; (3) the behaviour of an *Acraea* larva meeting successive ants, then not prepared to attack it; (4) the ants' *general* variability as to the food they would accept, rather surprising and reminding one somewhat of the different stages of hunger in a bird; (5) the release

of a *Mylabris* from a drive into which it had been carried, and the ejection, long after taking, of a number of *Antestia*; (6) the apparent failure to grasp glossy *Epilachna*—yet on one occasion some were carried off; (7) the earthing or leafing up of highly unacceptable objects (for the treatment of Acraeine eggs in the same way see below). One felt that it *ought* to have been for visual effect, yet of course it could not have been. The leaflets and earth-crumbs may have been specially scented by the ants, but why should it not have been sufficient to do this to the animal itself, as was apparently done in the tick-incident yet to be described? Experiments of this kind lead one to wonder, throughout, at the completeness with which other faculties are capable of taking the place of vision.

At any rate several animals—the fly, the larvae of *Acraea* and *Amauris*, the pupa of the latter (which was highly interesting), adult *Mylabris*, *Epilachna*, *Psammodes* (through hardness) and *Antestia*, all of them (unless *Antestia?*) with habits that place them at the mercy of *Dorylus*—probably the greatest scourge of relatively low-dwelling insect-life we possess—proved to be highly protected against it; and *Dorylus is* such a scourge that its attacks and its failures may reasonably be regarded as having aided appreciably in the selection (to their present high pitch) of these insects' protective qualities.

Of the potential prey itself, it is sufficient to say that all the animals just named except *Antestia* are highly sluggish and indifferent to attack. *Antestia*, our greatest coffee-pest, less so. It possesses a strong "bug" smell, and is conspicuously coloured, but it drops and flies and dodges round twigs somewhat readily. Even so, it is not very hard to catch, my coffee-girls bringing in great numbers daily when destroying them by hand-picking. It probably has special enemies: one of my tame but unconfined ground-hornbills (*Bucorax caffer*) once ate 193 in quick succession, and "capped" them with an *Amauris albimaculata*. We have also seen in the present experiments how *Dorylus* accepted them relatively readily, once in large numbers, though it subsequently did eject them.

In general, given that *Dorylus* readily accepts insects as low-grade as the *Acraeinae* and *Danainae*, the ants' acceptances and refusals come in line with those of my birds; for the latter too placed these butterflies above,

e. g., *Epilachna* and the larvae of *Acraeinae*, of *Danainae* and of certain other butterflies. This, on such general considerations as I have alluded to above, is only what one might expect. What, on those same considerations, one would *not* expect is that *Zonocerus* and *Rhodogastria*, both far more sluggish and apparently helpless than any of our *Danainae*, etc., should have been as readily accepted by the drivers, and placed slightly *above* the *Danainae* and *Acraea areca* by my birds.

2. Experiments with Insects' Eggs

April 28th, 1913.—A horde of the driver-ants had retired in the evening into their "drive," but at every opening there were warriors standing sentry with up-raised open jaws, and a few ants were walking about aimlessly or resting. I put down four eggs of *Acraea caldarena* attached, as laid, to a small scrap of *Wormskioldia* leaf. They were closely inspected by several ants, but no attempt was made to take them. I then added an egg of *Papilio dardanus* ♀ f. *hippocoon*. This attracted less attention: one warrior took it listlessly in his immense mandibles and, as I found afterwards, must have used just enough force to separate it from its leaf (*Teclea*), then left it without having damaged it. An egg of *Pseudacraea lucretia* var. *expansa* was also ignored.

April 29th.—This morning I visited an active column of *Dorylus*. The ants were keeping to their narrow-column formation and travelling rapidly, mostly in the same direction. I put down three eggs of *Acraea aglaonice*. These were examined by many ants but not attacked, and soon became shifted to the side of the column, amongst the guards. I then put down two eggs of *Pyrameis cardui*. The ants took absolutely no notice of these, merely scurrying over them, and they too had soon found their way to the side. A *P. hippocoon*'s egg followed. It remained unheeded too, but it formed a good-sized obstacle, and soon a passing ant picked it up and deposited it outside, then returned to the column without it. Two more eggs of *P. cardui* followed the example of the first two. All eggs in this experiment had been separated from their leaf before being offered. Were the eggs all definitely unacceptable to the ants? Were they too small to be worthy of notice? Were the ants too busy otherwise

at the moment to take notice of food? or (an unlikely supposition) were the eggs (one of which had been treated as an obstructing pebble might have been) regarded as of the mineral or vegetable kingdoms? I returned to the house and cut up a small piece of meat into scraps as small as a *P. dardanus* egg, and twenty minutes later returned to the ants.

The meat scraps were becoming dry. I put one in the track, and it was at first passed over, then seized and thrown outside as the *dardanus* egg had been. A second piece was treated in the same way. But a moist, freshly-extracted egg of a smallish, dull-coloured grasshopper was at once picked up and carried along, as was a freshly-cut-off piece of meat four times the size of a *dardanus* egg. But a similar piece of half the size was thrown outside! However, on my returning it, it was at first for a time passed by, then an ant took it and kept with it in the column. An egg of another species of grasshopper was set on to by three or four ants, and it was some time before one of them finally carried it along in the column. I then crushed and put in together three eggs of *A. acara*. They were picked up and carried along. To test what the ants were prepared to rise to in the matter of unpleasantness I next placed an adult *Acraea terpsichore*, L. (the only *Acraea* I had with me), first killing it, three or four inches from the column. It was quickly found, a mass of ants covered it up, the wings were gradually taken off at the base and the body brought into the column and carried along.

May 1st.—Again tried *Dorylus*—yesterday's column, as active as previously. I put in in turn slightly developed, unbroken eggs of *Papilio dardanus*, ♀ f. *hippocoon*, *Papilio demodocus* and *Pyrameis cardui* (four or five of this). They were in each case either completely ignored or merely picked up and dropped outside. Eggs of *A. acara* and *A. aglaonice*, put down two or three together, were completely and continuously neglected. I watched for quite half an hour, occasionally moving the eggs back into the run, but nothing other than what I have described occurred. But an egg of *Charaxes ethalion* (new-laid, plain green and not yet ringed) almost immediately found a carrier, and was taken along to the next outpost in the direction in which the main body was moving.

Two eggs of *hippocoon* extracted from the body of their

parent and placed still wet in the run attracted much more attention. Many ants examined them and some went so far as to enclose one or other with their mandibles, but each time at once desisted and went on.

After waiting for some time longer I collected all the eggs, then broke slightly two or three eggs of *A. aglaonice* and put them in together. They were largely ignored, but occasionally examined, and they found no carrier. A similarly-prepared *P. demodocus* egg was treated in the same way and of the two extracted *hippocoon* eggs one eventually found a carrier, being taken by a small worker with immense difficulty *against* the main current right back to the station the latter was leaving, nearly three yards off. An interesting incident occurred at the outset—all the more interesting because the ant was sightless : she had the greatest difficulty in making any headway, and eventually dropped out to the side and, waiting till three or four large ants with good-sized loads came along in the desired direction, fell in behind them. She was unable to keep up with them for very long, but eventually reached her goal. The other extracted *hippocoon* egg was finally picked up and thrown outside the column. Eggs of *P. cardui* (three or four partly broken and forming one mass) were examined, picked up and carried along, but two unbroken eggs of *C. ethalion* were ignored (as were, still, the broken eggs of Acraeas, etc., the treatment of which I have just described). On being broken, however, the two *Charaxes* eggs, one new-laid, the other already with a dark apical ring, each quickly found a carrier. A large adult male *Acraea doubledayi*, killed by myself and placed outside the column, was overwhelmed, diswinged, and carried away.

I added more *Pyrameis* eggs, but the rush of ants was now very great, and it was possibly for this reason that the eggs were continuously overrun, apparently unnoticed. So I turned my attention to one of the side columns. Here eggs of *A. aglaonice*, broken together, received a great deal of attention but found no carrier; a new-laid egg of *C. ethalion* was soon picked up and carried by a side connection into the main column; eggs of *A. acara* were treated exactly as those of its congener had been, but three or four *P. cardui* eggs were picked up together and carried to the station ahead; an egg of *P. demodocus* was treated as the *Acraea* eggs had been, but a semi-

incubated *ethalion* egg found a carrier. Thinking I might have crushed the *demodocus* egg so much as to render it unattractive by loss of contents I added another of the same brood very slightly crushed (in each case by pressure of a pin-point). This too was much examined but not taken, and one ant picked it up and dropped it outside the run. On my returning it, the egg was treated as before, but eventually an ant carried it for about eight inches, then once more deposited it outside. The *Acraea* eggs also remained untaken all this time, though frequently examined, but, on my putting down two *Pyrameis* eggs with a third of the same species crushed against them, they (the *Pyrameis* eggs) were picked up by a small ant and carried forward to the station. A further batch of two or three *Pyrameis* eggs was ignored, and the next half-incubated *ethalion* egg was examined by two or three ants and neglected. Whether these eggs would have continued to be neglected I am unable to say, as I had now to discontinue the experiment.

This description gives no real idea of the tediousness of the experiment, which lasted about two hours. In almost every case the egg was passed over by far more ants than noticed it, and the difference between the eggs of the Papilios and the Acraeas on the one hand and those of the two Nymphalines on the other, was that whereas the former were very frequently examined they remained untaken to the end, while the *Charaxes* and *Pyrameis* eggs were picked up and carried by the first or nearly the first ant that stopped to notice them.

I should say the *C. ethalion* eggs found carriers more readily than *Pyrameis* eggs. I was unable to find, for the broken-egg experiment, the half-incubated *hippocoon* egg I had used previously.

In view of *Acraea* eggs having been accepted the day before yesterday, their rejection in this experiment requires confirmation.

[On leaving the ants I found a medium-sized cattle-tick (*Rhipicephalus* sp.), and going back put it in the run. Some ants ran over it without stopping; one or two halted and examined; then one took it by the side and retiring to the side of the column held it there, merely preventing it from moving away, herself in meantime lying over on her side. As the stream of ants went ceaselessly past a number of its members—one at a time, two at a time, or

several at a time—would fall out, examine the tick well and then pass on. The examination frequently ended up with the adpression of the end of the ant's abdomen to the surface of the tick. I had previously seen them do this to some of the eggs when examining them, and once one ant did it to another. I watched the performance for quite fifteen minutes, and it was still going on when I left. Was it a demonstration to the younger generation of the distinctive characteristics of Mr. Tick? Or were they submitting their opinion of him? Or was he merely being detained until some official of the tick department should come along and take charge? !]

In the latish afternoon I returned to the spot and put down in turn in one of the smaller side columns the eggs (well-punctured) of the following butterflies :—*A. caldarena* (two lots of three or four each); *P. dardanus hippocoon* (two); *P. demodocus* (one); *P. cardui* (four, forming a single mass); *Eurytela hiarbas* (one); *Hypolimnas misippus* (two); and two *C. ethalion* (unusually small and yellow, not green, and with a very narrow ring). Throughout the experiment, which lasted a considerable time, I saw no notice at all taken of the hairy egg of *E. hiarbas*—it merely became automatically pushed out to one side each time I returned it to the column. I forget whether I saw the *Pyrameis* eggs definitely inspected—at any rate, they found no carriers and met with the same treatment as that of the *Eurytela*. At least once an *H. misippus* egg was inspected, but neither was taken. The *hippocoon* and *P. demodocus* eggs were always carried outside, never along, and at first the same was done to the two *C. ethalion* eggs. Seeing this, I added a green *ethalion* egg of the brood from which I had used in the morning. This quickly found a carrier. I added yet another and an egg of *P. lucretia* var. *expansa*. Each was shortly thrown outside, but only a few minutes later the *Pseudacraea* egg was again picked up, and this time carried right on to the next station.

The *A. caldarena* eggs were sometimes inspected and always refused, and so were some *A. acara* eggs that I now added, together with two more eggs of *Pyrameis* and another of *P. lucretia*. The *C. ethalion* eggs were being frequently inspected and occasionally picked up, but none were carried away, and once an ant, having inspected and refused one of them, passed on to the *P. lucretia* egg close by (it had been put outside the column by an ant which

had come into contact with it), and, after examining it, picked it up and carried it along with the column to the station ahead. I now put down close beside each other ten punctured eggs of *A. acara*, already turning purplish brown from incubation. My putting down so many in quick succession disturbed that portion of the column, and there was a very slight movement out in my direction, during which a number of ants came into contact with *Acraea* eggs and inspected them, in every case briefly and with rejection following. Two or three of them now set to work and placed small pieces of earth on top of the eggs, a good-sized piece of dry grass-blade crowning all. This has only been done in my previous experience to the most highly unacceptable of prey, and it constituted, I believe, the best possible evidence of the ants' definite repugnance to the eggs. After they had been thus branded, the eggs, though still visible to myself, were no longer, so far as I saw, the subject of examination. About this time the green *C. ethalion* egg found a carrier. Rather earlier in the experiment the *P. demodocus* egg was taken up, though lying outside the column, by an exceptionally small ant. The nearest sentry at once came up and inspected, and before the small ant finally got well away the egg twice or thrice became the object of inspection for three or four ants at a time; but she finally went off with it with the column.

I now left for half an hour. On my return things were much as I had left them, and none of the *Acraea* eggs had been moved. I decided once more to test the view that it was merely the small size of the eggs that was against them. I accordingly cut up two house-flies (*Musca domestica*) into fragments not larger than a *Papilio* egg (for example, the two eyes each constituted a different offering), and placed them in and near the run. Each piece at once became the prey of *several* ants, not merely of perhaps the fortieth chance passer-by as in the case of the accepted eggs, and all were quickly carried off. I added, each separately, the two eyes of a ♀ *A. caldarena*, and these were also taken. I then extracted its eggs (there were not very many) and laid them down as three or four little separate masses. The ants swarmed over them as over the previous offerings, but very speedily desisted and quickly covered them with small scraps of earth, after which they were persistently neglected. I

noticed too that the earliest eggs in the experiment—the *laid* eggs of *A. caldarena*—had, earlier, also been placarded in the same way. I then laid down, in three pieces each, the abdomen and thorax of the *Acraea*. These were seized by quite a number of ants, as was a whole, wingless, dead *A. caldarena*, but were not carried far, each being abandoned after a trip of a few inches. They were not placarded, at any rate to any noticeable extent. In the general bustle the earlier *caldarena* and *acara* eggs became uncovered, and they and at any rate the larger of the remaining eggs came in for a good deal of additional attention, and the remaining green *ethalion* egg was quickly carried off, as also one of the yellow ones. One *hippocoon* egg disappeared now or earlier, but may of course simply have become hidden by loose earth; the other remained untaken throughout and eventually fell into some debris in a rut, and I was unable to recover it. I saw none of the small Nymphaline eggs taken, and was able to find more than half of them at the end. I added a *P. demodocus* and a *hippocoon* egg during the bustle, and these were after much delay taken, and an egg of either *Charaxes brutus* or *C. cithaeron*, which was visited by many ants, and though a relatively large and conspicuous object and brimming over with liquid was each time merely tried and left. A green *C. ethalion* which I added to it was taken practically at once, and eventually the larger *Charaxes* egg found a carrier too. The uncovered *Acraea* eggs found many visitors but never a carrier, and on my visiting the ants again the last thing in the evening remained uneaten and had been partly earthed up again.

Before discontinuing the experiment I had added one or two small, black orange-Aphides by themselves, and, in a mass on the twig on which I found them, a large number of others. They attracted a great deal of attention, but I was unable definitely to see that the ants "milked" them at all, as do some of our other ants, but a few of the usual warning earth-crumbs were placed on them.

May 2nd.—During the morning, again going to yesterday's side-column, I placed by it several eggs of *A. caldarena* and *A. acara*. They were subjected to a great deal of inspection, and finally earthed and neglected. A *Danaida chrysippus* egg which I placed right in the ants' path was inspected by very numerous ants but always at once

refused. Eggs of *hippocoon* and *P. demodocus* were usually given longer consideration by the ants that stopped at them and, especially the latter, sometimes picked up, but were not taken. Of two *H. misippus* eggs only one, so far as I saw, was properly inspected, and it was refused. An egg of *E. hiarbas* was once or twice inspected and once picked up and put outside but not taken, and two or three eggs together of *P. cardui* were rejected. But a *C. ethalion* of yesterday's yellow brood was at once picked up by the first small ant that came to it and carried away. The larva, only just hatched and not yet having eaten, of *hippocoon* was passed over for some time and several times inspected and refused, but finally an ant took it and held it in one place for two or three minutes while passers inspected it (as in the case of the tick) before she finally commenced definitely to carry it. She was even then very undecided for a time, sometimes going on towards the next station ahead, then retracing her steps and going towards the main column and so on. Finally, she took the latter direction.

I kept moving the rejected eggs back as they became pushed or carried to the side, but without effect, though a fresh green *C. ethalion* egg that I added to them was at once taken and carried, and eventually an ant took the *P. demodocus* egg and, after what looked like much consultation, carried it off too. I now turned my attention to the main column, which was going strong, nine or ten abreast. I put in the *Danaida* egg. It was inspected and at once rejected by several ants, and at last put out to the side and well earthed up. A *P. dardanus hippocoon* egg was twice ejected, two eggs of *A. acara* were ejected after having been the subject of much inspection by individual passers-by, and earth-crumbs were placed against them. But a yellow *C. ethalion* egg was quickly picked up and carried to the nearest station.

On my bringing *Danaida* to the more active attention of the ants it was several times tried with the antennae and refused, the *hippocoon* egg, as well as a second that I added, was persistently ignored or ejected; the *P. demodocus* egg was tried and refused a few times, then found a carrier; of two *P. cardui* eggs put down, one was picked up very soon and carried along, the other remained ignored and possibly unnoticed; two eggs of *H. misippus* placed amongst the ants were overrun and gradually

drifted to the side every time I brought them back. I did not see them tried. An *E. hiarbas* egg was picked up and ejected, as was, several times, an egg of *hippocoon* and one of *P. demodocus*; but a green egg, with dark ring, of *C. ethalion* was very soon picked up and carried with the column. I then killed, diswinged and put just inside the column a ♂ *D. chrysippus* and a ♂ *Acraea natalica*. Each was at once covered by a mass of ants and gradually brought into the line. Proceedings continued to be so slow that I had to leave, but on my return to inspect half an hour later or less both had completely disappeared.

May 2nd.—Afternoon.

This was really a larva experiment, but as eggs were used too, and as the use of freshly-hatched larvae is also obviously relevant, I ought perhaps to state the gist of it here.

Eggs of *A. acara* many times refused, one each of *hippocoon* and *P. demodocus* two or three times ejected, a just-hatched *P. dardanus* larva treated as in the morning, but a three-quarter-grown one with the final, most protective appearance at once set upon and carried off. Barely hatched *A. acara* larvae, still busy with their egg-shells, persistently refused and repeatedly ejected, but a half-grown individual of the same species killed and taken, as also quarter-grown *E. hiarbas* and *A. caldarena* larvae and a nearly full-grown *A. caldarena* larva.

The larger *Acraea* larvae gave the ants a good deal of trouble by exuding, when set upon, drops of the usual poppy-flavoured liquid from the ends of their bristles. They thus succeeded more than once in escaping from the column. I put them back, however, and the ants overcame the difficulty intentionally or incidentally by placing on the ends of the bristles crumbs of dry earth, which soaked up the liquid and enabled them to bite off the bristles lower down. Fresh drops appeared as the result of this, and fresh crumbs of earth were applied until finally the bristles were razed off level, in many cases, with the caterpillar's body. It was then set upon freely by masses of ants, killed and carried off. I at first believed that the application of the earth-crumbs was purely in the nature of "placarding" (which is still possible), but I felt before the end of the experiment that it might readily be, as I have described it, for the purpose

of soaking up the liquid. I hope to repeat the experiment. The greater repugnance shown for the very young larvae is of great interest. It is in line with the dislike shown for the eggs, and perhaps explains the greater conspicuousness of certain newly-hatched larvae — for instance, those of *Papilio dardanus*. It is also in line with native statements about nestling birds (alleged to be in general less pleasant to eat than the adults), though this has not been proved to apply to other enemies than man.

In a weak column of ants elsewhere I had tested a few days previously larvae of *Acraea caldarena* (from a quarter to nearly full-grown) against larvae of *Precis natalensis* of the same sizes, also against a dull-coloured spider that I happened to catch on the spot. The *Acraea* larvae escaped by the use of the fluid secretion, but the *Precis* larvae and the spider were killed and carried off.

May 3rd.—Put down an *Atella phalantha* egg. Numbers of ants passed over it, but none stopped to examine. Finally it suddenly disappeared. It must, I think, have been picked up, but whether thrown out or carried along I could not ascertain. A second was for some time passed over unheeded in the same way, until suddenly a small worker picked it up, dropped it quickly just outside and passed on again. On my returning it, the egg was again passed over as before and remained untaken when I had to leave, a few minutes later.

May 6th.—Put down two eggs of *Charaxes candiope*, already lightly ringed. They were passed over and examined and neglected by a number of ants, until finally an ant examined one of them thoroughly, picked it up and going a few inches down the column turned into an out-jutting "creek" (so to speak) of ants, scrambled in amongst the others, possibly consulting, came out again and a few inches back the way she had come, then back again into the little conclave, out again and back yet again. On her emerging this time my attention was diverted to a prolonged examination that was taking place of the second egg, and I could not again trace the first, so am unaware of its eventual fate. I added two more *C. candiope* eggs to the second (the examination of which had ended in ejection from the column), also two eggs each of *P. demodocus*, *Atella phalantha* and *hippocoon*, and four or five (together) of *A. acara* (dark with incubation). I

watched for a long time and, though many examinations and one or two apparent consultations took place, none of the eggs were taken, and the larger ones usually ended in being ejected each time I put them in. I then put down an egg of *C. ethalion*, with a ring and slightly incubated. It was very soon picked up and carried along to a tunnel, but a second of the same date received much the same treatment as the other eggs.

The above took place in the orderly bustle of a marching column. I next went to the head of a column some distance away, where the ants were well scattered out over a wide area, searching, and put down on a stone they were crossing two eggs of *C. candiope*, one of *hippocoon*, one of *P. demodocus* and one of *A. phalantha*. They were many times examined but never taken. I added an egg of *C. ethalion*, and after being examined and left, like the others, a few times, it was picked up and carried for a distance, then put down. On my replacing it, this egg (and none of the others) was soon picked up once more and carried away. I now kept trying to bring a *C. candiope* egg to the notice of the ants and it was always refused though often examined, but a *C. ethalion* (very hard-set) was then treated similarly. There were very few ants here now, and I next went on to experiment at a spot where they were covering the ground fairly thickly, and put down an egg of *C. candiope*. This was set upon by several ants, but they shortly desisted and left it, and treated similarly two more eggs of the same species. A *P. dardanus hippocoon* egg, a *P. demodocus* egg, an *A. phalantha* egg and eggs of *A. acara* were also all refused, as was the about-to-hatch *C. ethalion* egg. The ants were already becoming thinner again at this point, so I moved the eggs and added a fresher *C. ethalion* egg, marking the place. I left, and returned ten minutes later to find that the ants had shifted on again, leaving all the eggs as they had been put down by myself.

I decided at this point to discontinue the experiments. I had not the animals for the far more extensive series of experiments that I still hope to undertake, and the ants' reply to the question asked of them had been in any case of a sufficiently consistent nature so far as they themselves were concerned. In spite of their rather catholic tastes, they had evidently found all the eggs offered them—at all events all they definitely tried—rather highly un-

acceptable, but not quite equally unacceptable. I am inclined to state as follows the grades that were indicated :—

(1) *Pseudacraea lucretia* var. *expansa* and *Charaxes ethalion*.
(2) *Papilio demodocus*. } *Charaxes cithaeron*.
(3) *Papilio dardanus*. }
(4) *Acraea acara*, *A. aglaonice*, *A. caldarena* and *Danaida chrysippus*.

Pyrameis cardui eggs would appear from at least one experiment to be preferred to those of *P. dardanus*, but they cannot, I think, be very *much* higher. *Hypolimnas misippus* and *Eurytela hiarbas* eggs would appear to be as low as that of *P. dardanus*, but the extent to which they were genuinely tried seems doubtful.

The eggs tested cover quite a considerable range of appearance, and this, with the fact that when we ourselves search for it with the closeness that is habitually employed by its natural enemies we have relatively little difficulty in finding the average leaf-laid egg, at least suggests that it is not amongst such eggs but amongst those that are concealed in earth, stems, etc., that we must look for the higher grades of palatability. The inference that it was through repugnance to them that the ants avoided the eggs was confirmed by their repugnance to newly-hatched larvae as compared with older ones.

3. Experiments on Cockroaches, a Cricket and a Coccinellid.

April 28th, 1913.—Early in the day I placed in a small gauze-covered box with two live larval cockroaches thirteen eggs of *Acraea aglaonice*, twelve of *Acraea caldarena*, ten of *Pyrameis cardui* and three of *Papilio dardanus* ♀ f. *hippocoon*. None had been eaten by evening, and during the evening the cockroaches escaped. I replaced them at about 10 p.m. in the evening by two adult and three larval cockroaches of the same species.

I left in another small box with a female of the carnivorous ladybird *Alesia bidentata* a number of eggs of *A. caldarena*, three of *hippocoon* and one of *P. cardui*.

[Cockroaches were of our common Gazaland species.]

April 29th.—No developments in the cockroach box. In the other box the *Alesia*, instead of eating the egg, has

merely added to them one of her own. It is laid beside the *Acraea* eggs on a small bit of green *Wormskioldia longipedunculata* leaf.

April 30th.—Removed the eggs supplied to the *Alesia*, since she continued to refuse them, and placed them in a gauze-covered box with a carnivorous cricket (*Arytropteris* sp.).

May 1st.—No developments in the cockroach and cricket boxes except that the former insects, while still ignoring the eggs, had eaten a portion of a dead companion.

Later.—The cockroaches and cricket persisted in refusing the eggs, not only when unbroken but when damaged by a pin-point. One actual tasting followed by a rejection took place on the part of one of the cockroaches, and eggs extracted from a *hippocoon*'s body were refused. But both cockroaches and cricket ate other food that I eventually offered them, including eggs extracted from small dull-coloured grasshoppers.

Concluding Remarks.—The experiments, were they made on better-chosen enemies, would suggest that openly-laid lepidopterous eggs, generally, are somewhat highly protected by some such quality as nauseousness, though in varying degrees. It was interesting that the egg most frequently taken was a leaf-green one.

As it is, the experiments are open to criticism. Yet they suggest that experiments on visually-discriminating egg-enemies may be well worth carrying out. So far as the parasitic Hymenoptera are concerned, facts have been recorded showing that some, at any rate, of these do *not* recognise eggs visually.

Should further experimentation produce the results that I am inclined to expect, the study of the appearance of insects' eggs is likely to be a very fascinating one. Nor will it be entirely dependent on the obtaining of the food-plant. Thus I have compared the *laid* eggs of quite a number of different species of butterflies with the most advanced eggs still in the bodies of the gravid parents, and I have found that in each case the eggs about to be laid corresponded well in colour and form with newly-laid eggs.

Against this we have the fact that newly-laid eggs—and therefore also eggs extracted from the parent's body—do not necessarily give an accurate idea of what will be the coloration of the egg during the greater part of its existence as such; for many eggs (as those of *Papilio* and

Charaxes) do not attain their full coloration for a day or two after laying, and they darken again when approaching hatching. Yet even here something may be done; for I have found (my observations here being confined, however, to species of the three genera *Pseudacraea*, *Charaxes* and *Papilio*) that a gravid female at death usually contains one fertile unlaid egg, and that this egg, but not the others, goes through its colour-changes within the parent's body (or if extracted from it) just as it would have done after laying, and ends (if the parent's drying be not too rapid) in actually hatching therein. I have taken a live larva, half out of its shell, from the body of a long-dead *Pseudacraea lucretia* var. *expansa*, and it has fed freely when placed on *Chrysophyllum fulvum* (its food-plant in the Chirinda forest) and has quickly proceeded to cover itself in the normal manner with its own frass.

The one fertile egg has of course another obvious application. It may enable us to study the life-history of an insect that has proved refractory about laying. I have bred *Papilio dardanus* from such eggs, and the *Pseudacraea* larva referred to above was already more than a week old and strong and vigorous when it was unluckily accidentally killed. I have, I believe, twice obtained more than one such egg (in each case from a dead *P. dardanus* ♀ f. *hippocoon*) as against more than thirty instances in which there was only one.

[For Mr. Swynnerton's further notes on the eggs of butterflies see Supplement, p. 428.—E. B. P.]